

New record and phylogenetic assessment of *Apopharynx bolodes* (Braun, 1902) (Digenea: Psilostomidae), a parasite of Eurasian Coot *Fulica atra* Linnaeus, 1758 (Aves: Rallidae)

Short Communication

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Abstract

Phylogenetic studies of aberrant species are of considerable scientific interest because their taxonomic rank in traditional systems based on morphological characters is not infrequently overestimated. *Apopharynx bolodes* (Braun, 1902) is one of the few psilostomid digeneans devoid of the pharynx. This is considered a sufficient basis for assigning it and similar species to the subfamily Apopharynginae. We found *A. bolodes* in *Fulica atra* Linnaeus, 1758 from Belarus, described it morphologically, and genotyped it by the 28S rRNA gene and the ITS2 region. It is the first molecular data on *A. bolodes* and the first record of this digenean species in Belarus. The phylogenetic analysis based on partial sequences of the 28S rRNA gene showed that *A. bolodes* is closely related to the *Sphaeridiotrema* spp. (*Sphaeridiotrematinae*). However, this phylogenetic inference has not received yet support with data on the ITS2 region.

Introduction

Eurasian Coot *Fulica atra* Linnaeus, 1758 is a wetland bird widespread in the Palearctic. Its diet may vary depending on habitat and season but is generally characterised by the predominance of aquatic plants over animal prey (Delić 1990; Perrow *et al.* 1997; Mouronval *et al.* 2007; Metna *et al.* 2015; Sakai 2015). This feeding pattern favours infection with psilostomid and notocotyloid digeneans, whose larvae, adolestocariae, encyst in the environment, often on aquatic plants, and are consumed by coots together with them.

The Psilostomidae is a relatively small family of the Echinostomatoidea, whose adults parasitise mainly wetland birds (Kostadinova 2005; Tkach *et al.* 2016; Kudlai *et al.* 2017). Taxonomic structure and composition of this family requires revision (Tkach *et al.* 2016; Kudlai *et al.* 2016, 2017; Kalinina *et al.* 2022). To date, eight species of the Psilostomidae have been recorded in the Eurasian Coot: *Apopharynx bolodes* (Braun, 1902), *Psilochasmus oxyurus* (Creplin, 1825), *Psilostomum brevicolle* (Creplin, 1829), *Psilostomum fulicae* Ricci & Carrescia, 1961, *Psilotrema oligoon* (von Linstow, 1887), *Psilotrema simillimum* (Mühling, 1898), *Psilotrema spiculigerum* (Mühling, 1898), and *Sphaeridiotrema globulus* (Rudolphi, 1819) (e.g. Pukhov 1939; Bykhovskaya-Pavlovskaya 1953; Ricci and Carrescia 1961; Macko 1968; Filimonova & Shalyapina 1975; Iskova 1985; Serbina 2006; Sitko *et al.* 2006; Niewiadomska 2015). Four of them (*P. brevicolle*, *P. simillimum*, *P. oxyurus*, and *S. globulus*) have been studied using molecular methods, though all genotyped isolates were derived not from Eurasian Coot but from other hosts.

Of representatives of the Psilostomidae parasitising Eurasian Coot, *A. bolodes* is of a particular interest. It is the type and only species of *Apopharynx* Lühe, 1909, which, in turn, is the type genus of the Apopharynginae Yamaguti, 1958 (Yamaguti 1958, 1971; Kostadinova 2005). The differentiating feature of this subfamily is the absence of the pharynx (Yamaguti, 1958, 1971; Byrd & Prestwood 1969; Kostadinova 2005). In addition to the type genus, the Apopharynginae includes *Psilotornus* Byrd & Prestwood, 1969 (Byrd & Prestwood 1969; Yamaguti, 1971; Kostadinova 2005), whose representatives, like *A. bolodes*, have not yet been genotyped either. Molecular data on this subfamily are much needed for the future revision of the Psilostomidae.

In this paper, we report the presence of *A. bolodes* in Eurasian Coot in Belarus and assess the phylogenetic position of this parasite species.

Materials and methods

Two adult specimens of *A. bolodes* were collected from the bursa of Fabricius during parasitological study of individuals of Eurasian Coot (n = 15) shot by licensed hunters at Lake Naroch

near Naroch Village (Minsk Region), Belarus (54°54'8" N, 26°44'37" E), in September 2023. Digenean specimens were relaxed in fresh water, fixed with 70% ethanol, and, after a few minutes, transferred to 96% ethanol. These parasites have subsequently been studied by morphological and molecular techniques. For the morphological study, the specimens were stained with acetocarmine, dehydrated in a graded ethanol series, cleared with dimethyl phthalate, and finally mounted in Canada balsam. All the measurements are given in micrometres (μm). The drawings were made with the help of the camera lucida. Voucher specimens of *A. bolodes* (hologenophore and paragenophore) are stored in the personal collection of the first author.

DNA was extracted separately from small body fragments of two specimens of *A. bolodes* according to Holterman *et al.* (2006). BIO-RAD T100 Thermal Cycler amplified the fragments. Polymerase chain reactions were performed in a total volume of 25 μL using the Encyclo Plus PCRkit (Eurogene) according to the manufacturer's instructions. Partial 28S rRNA gene sequences were amplified with ZX1aF (5'-ACCCGCTGAATT-TAAGCATAT-3') (Palm *et al.* 2009) and 1500R (5'-GCTATCCTGAGGGAACTTCG-3') (Tkach *et al.* 1999) primers. The following protocol was used: initial denaturation at 95 °C (5 min); 40 cycles of 30 s at 95 °C; 30 s at 55 °C; 2 min at 72 °C; and 7 min at 72 °C for the final extension. To amplify the complete sequences of the ITS2 region, we used 3S (5'-GTACCGGTGGATCACGTGGCTAGTG-3') (Morgan & Blair, 1995) and ITS2.2 (5'-CCTGGTTAGTTTCTTTTCCTCCGC-3') (Cribb *et al.*, 1998) primers, according to the following protocol: cycle 1 was 95 °C for 3 min, 45 °C for 2 min and 72 °C for 150 s; this was followed by four shorter cycles, 95 °C for 45 s, 50 °C for 45 s and 72 °C for 90 s, then a further 30 cycles of 95 °C for 20 s, 52 °C for 20 s, and 72 °C for 90 s and 5 min at 72 °C for the final extension. Unfortunately, amplicons could be obtained for only one specimen. All attempts to amplify markers of mitochondrial DNA (cox1 and nd1 genes) in *A. bolodes* using various primers were unsuccessful.

For the phylogenetic reconstructions of *A. bolodes* based on the 28S rRNA gene datasets, the newly obtained sequence was aligned with those of 22 psilostomid species available in GenBank NCBI (Table S1). Only sequences exceeding the length of 1000 bp were used for the 28S rRNA gene-based analysis. When we generated a tree based on complete sequences of the ITS2 region, the newly obtained sequence was aligned with those of the six psilostomid species from the NCBI GenBank (Table S1). The general alignments of partial sequences of 28S rRNA gene and complete sequences of ITS2 region were generated with "MAFFT" v7.520 (Katoh & Standley 2013) as implemented in Conda environment (Anaconda Software Distribution 2020), and then checked manually in SeaView Version 4.0 software (Gouy *et al.* 2010). The evolutionary model was estimated with the help of jModeltest 2.1.7 (Darriba *et al.* 2012). The best fitted model was GTR+G+I for analysis based on the 28S rRNA gene dataset, and TVM+I model for analysis based on the ITS2 region dataset. Bayesian Inference analyses were performed in MrBayes 3.2.7a (Ronquist *et al.* 2012) at CIPRES (Miller *et al.* 2010) portal for 15,000,000 generations and the first 25% generations were discarded for burn-in. Representatives of the Notocotylidae were used as an outgroup following Kalinina *et al.* (2022).

Results

Apopharynx bolodes (Braun, 1902) (Figure 1). Description (based on one hologenophore and one paragenophore). Body fusiform,

1742–2309 long, with maximum width just anteriorly to midbody, at least 795–894 (right margin of body was cut off and used for DNA extraction). Tegument spinous. Forebody 37.6%–38.7% of body length. Oral sucker almost rounded, subterminal, 282–324 wide, mouth opens ventrally. Preoral lobe distinct. Ventral sucker almost rounded, 272–307 \times 269–310. Sucker width ratio 1:0.95. Prepharynx and pharynx absent. Oesophagus 287–290 long. Intestinal bifurcation in third quarter of forebody or at border between third and posterior quarters of forebody. Caeca terminating blindly near posterior extremity of body. Testes two, tandem, smooth, partly overlapping; anterior testis rounded or almost so, 277–404 \times 278–439, in anterior half of hindbody; posterior testis suboval, 295–367 \times 241–280, in anterior half of hindbody. Post-testicular field 7.4%–8.6% of body length. Cirrus-sac elongate-oval, 242–376 \times 115–116, anterior to ventral sucker. Internal seminal vesicle tubular, convoluted. Pars prostatica tubular when cirrus everted; surrounded by prostatic cells. Cirrus unarmed, oval in everted state. Common genital pore sinistro-submedian, between mid-level of oesophagus and intestinal bifurcation. Ovary rounded or almost so, 148–218 \times 147–239, median or slightly dextro-submedian, pretesticular, contiguous with or partly overlapping anterior testis, contiguous with or posterior to posterior margin of ventral sucker. Laurer's canal opens antero-sinistro-dorsally to ovary. Oötype with Mehlis' gland antero-sinistral to ovary. Uterus pre-ovarian. Proximal part of uterus acts as uterine seminal vesicle; distal part terminates with sphincter, opens into genital atrium dorsally to male genital pore. Eggs deformed in balsam; length of least-deformed eggs 95. Vitellarium follicular; follicles in two lateral fields between intestinal bifurcation and posterior margin of posterior testis; not confluent. Vitelline reservoir at level of posterior margin of ovary. Excretory vesicle Y-shaped, with stem extending to posterior margin of posterior testis; pore terminal.

In phylogenetic analysis based on partial 28S rRNA gene sequences, *A. bolodes* (GenBank NCBI accession number PP848221) was a weakly supported sister to the *Sphaeridiotrema* spp. clade, which was also weakly supported (Figure 2). In turn, *A. bolodes* + *Sphaeridiotrema* spp. clade had a poorly supported sister relationship with the strongly supported *P. oxyurus* + *P. brevicolle* clade. The clade including all the species mentioned above was a strongly supported sister to the poorly supported clade, which was in turn subdivided into the poorly supported group containing *Macracetabulum albeolae* Kudlai, Kostadinova, Pulis & Tkach, 2017, *Longisaccus elvirae* Kudlai, Kostadinova, Pulis & Tkach, 2017, *Byrdtrema sponsae* Kudlai, Kostadinova, Pulis & Tkach, 2017 and *Neopsilotrema* spp. and the strongly supported group containing *Psilotrema limosum* Kalinina, Tatonova & Besprozvannykh, 2022 and unidentified psilostomids from the study of Schwelm *et al.* (2020).

The phylogenetic tree based on complete sequences of the ITS2 region *A. bolodes* (GenBank NCBI accession number PQ164795) appeared as a weakly supported sister to *Neopsilotrema* spp. clade. The *A. bolodes* + *Neopsilotrema* spp. clade had the poorly supported sister relationship with *Psilostomum brevicolle* (Creplin, 1829). In turn, the clade of all these species formed the strongly supported sister relationship with *Sphaeridiotrema pseudoglobulus* McLaughlin, Scott & Huffman, 1993 (Figure 3).

Discussion

The trematode specimens examined in our study correspond to *A. bolodes* in all key morphological characters, namely, the body

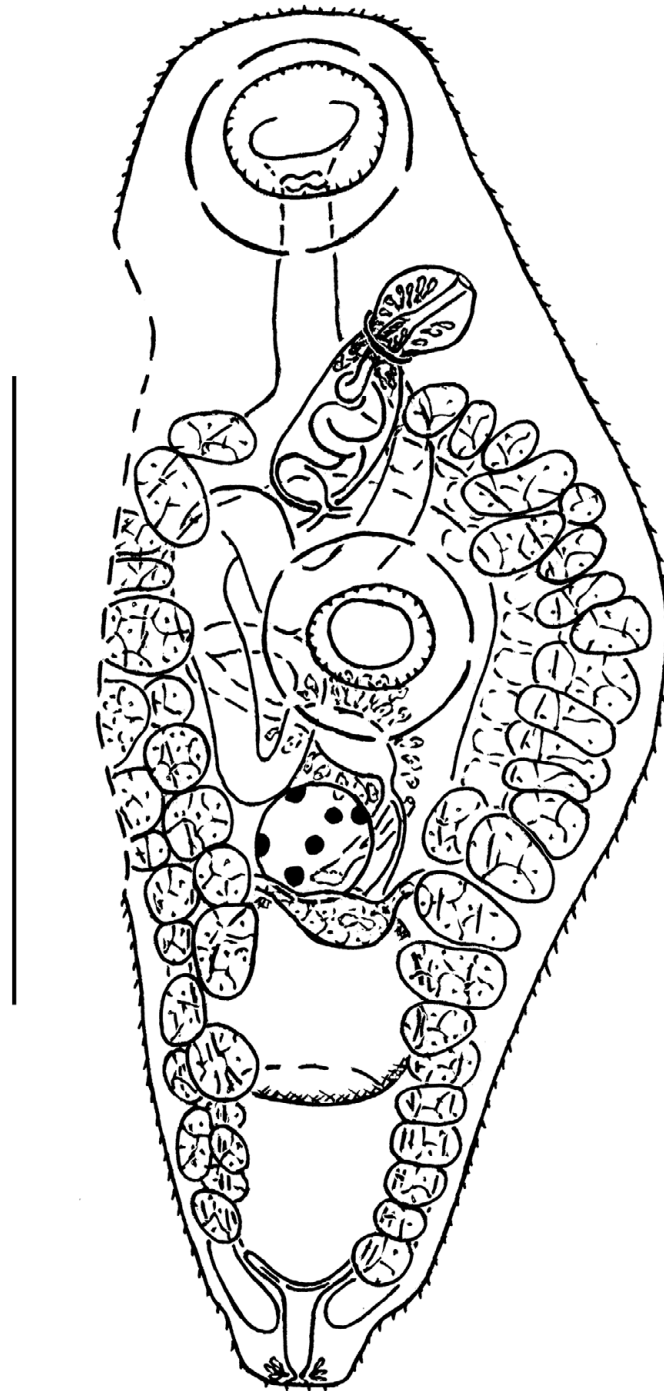


Figure 1. Hologenophore of *Apopharynx bolodes* from *Fulica atra*, Belarus. Scale bar, 800 μm .

shape, the absence of the pharynx, the position of the ventral sucker, the common genital pore, the cirrus sac and the gonads, and the distribution of the vitelline follicles (Braun 1902; Bykhovskaya-Pavlovskaya 1953; Kostadinova 2005). According to several authors, *A. bolodes* lacks not the pharynx but the oral sucker (Odhner 1913; Skrzjabin 1947; Odening 1962). However, following the concept of Kostadinova (2005), we believe that this species is actually devoid of the pharynx. Dimensions of the body, organs, and eggs in our specimens are similar to those reported for this species by other authors (Table 1).

This is the first report of *A. bolodes* from Belarus. This parasite species has previously been found in Kaliningrad, Novosibirsk, and Rostov regions of Russia (Braun 1902; Pukhov 1939; Bykhovskaya-Pavlovskaya 1953; Filimonova & Shalyapina 1975; Serbina 2006), Hungary (Edelényi 1974), Poland (Sulgostowska 1960; Pojmańska *et al.* 1984), Slovakia (Macko 1968), and Germany (Odening 1962). In all cases, this parasite was found only in Eurasian Coot. The life cycle of *A. bolodes* has not been elucidated.

We obtained the first data on the phylogenetic position of *A. bolodes*. The 28S- and ITS2-based phylogeny we obtained here are

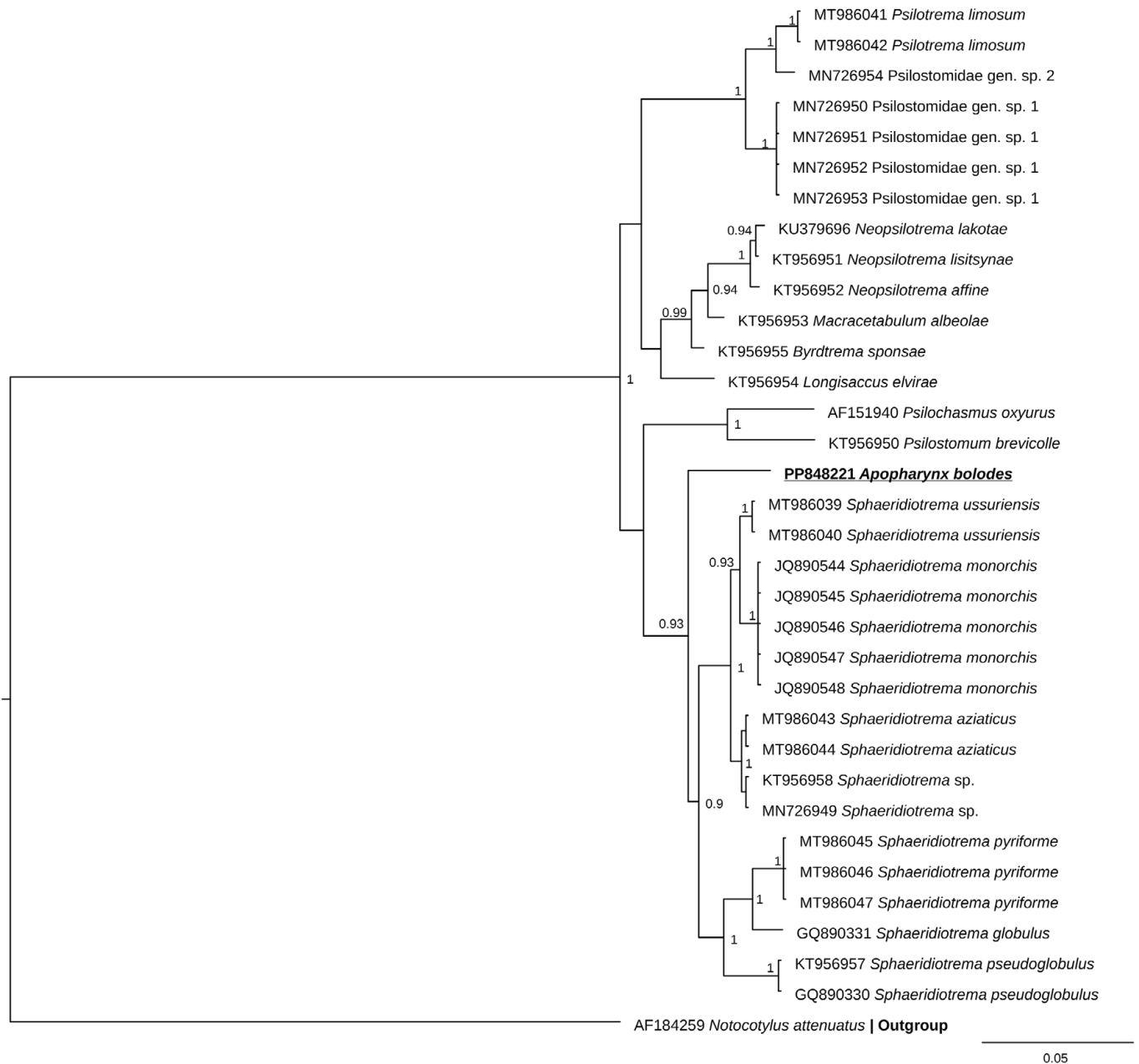


Figure 2. Phylogenetic relationships of *Apopharynx bolodes* reconstructed by Bayesian Inference analysis of 28S rRNA gene partial sequences. Posterior probability values lower than 0.9 are not shown. Newly obtained sequences are underlined.

not consistent with each other. However, they are, in principle, difficult to compare because of the sharply different number of species included in the corresponding analyses. The position of *A. bolodes* on the 28S-tree as a sister taxon to the *Sphaeridiotrema* spp. clade is supported by morphological data. Members of these two clades are similar in body shape and the distribution of the vitelline follicles (compare with Bykhovskaya-Pavlovskaya 1953; Kalinina *et al.* 2022). However, given the current results of the analysis of complete sequences of the ITS2 region, the close relationship of *A. bolodes* with the *Sphaeridiotrema* spp. clade requires additional molecular verification.

In traditional systems of the Psilostomidae, the aberrant morphology of *A. bolodes* and *Psilotornus* spp., that is, the absence of the pharynx, is considered a strong argument in favour of assigning

them to a separate subfamily, the Apopharynginae (Yamaguti 1958, 1971; Kostadinova 2005). However, this is the only argument supporting this hypothesis. The close phylogenetic affinity between *A. bolodes* and the *Sphaeridiotrema* spp. clade (*Sphaeridiotrematinae* Yamaguti, 1958) on the 28S-tree casts doubts on the necessity of assigning *Apopharynx* and *Sphaeridiotrema* Odhner, 1913 to different subfamilies.

All psilostomid species involved in our phylogenetic analysis based on the 28S rRNA gene dataset appeared to be distributed across three major clades, namely (i) *P. limosum* with *Psilostomidae* gen. sp. from Schwelm *et al.* (2020), (ii) *M. albeolae*, *L. elvirae*, and *B. sponsae* with *Neopsilotrema* spp., and (iii) *P. oxyurus*, *P. brevicolle*, and *A. bolodes* with *Sphaeridiotrema* spp. These results are congruent with the clustering of psilostomids in Kalinina *et al.*

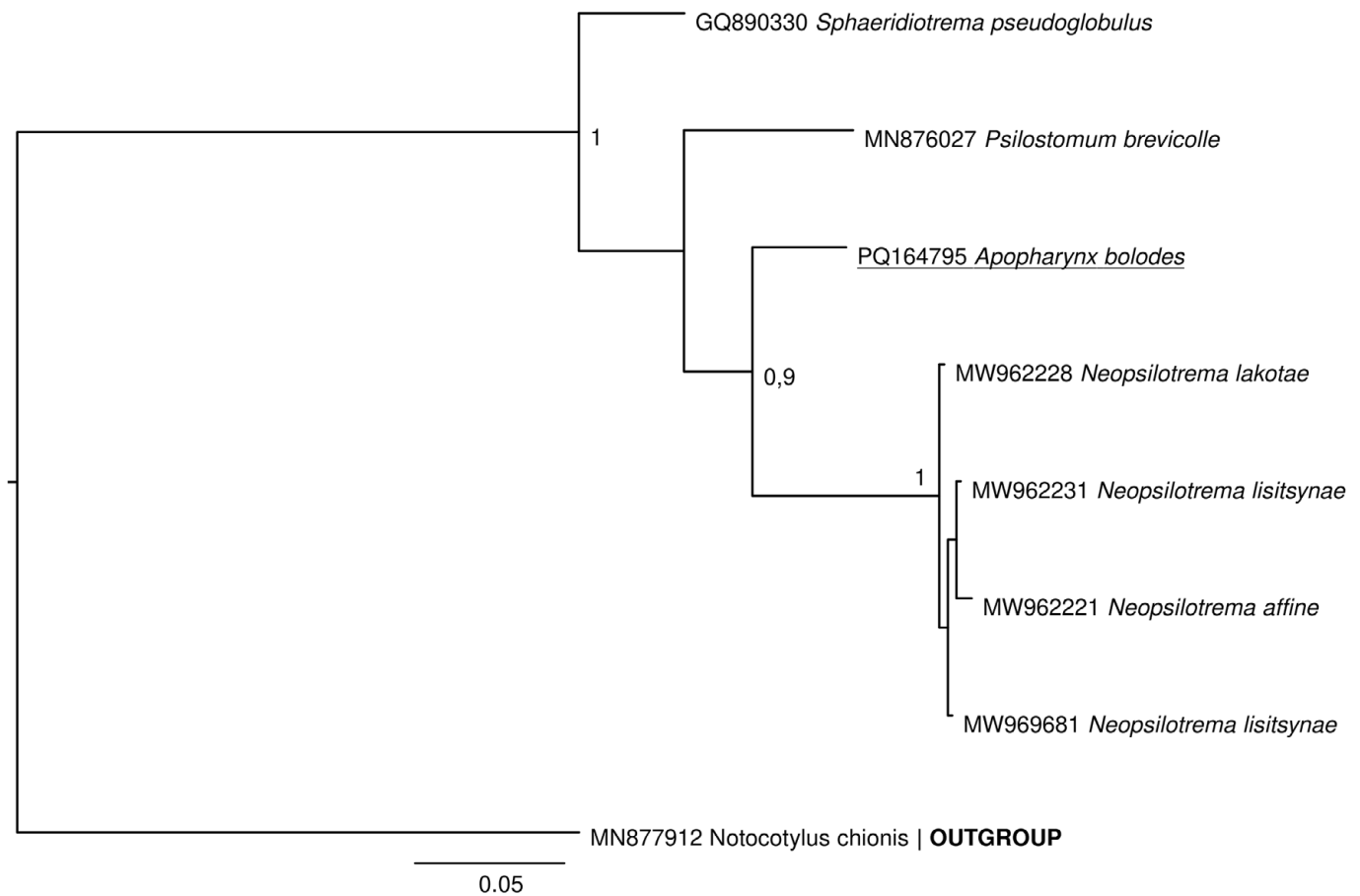


Figure 3. Phylogenetic relationships of *Apopharynx bolodes* reconstructed by Bayesian Inference analysis of ITS2 region complete sequences. Posterior probability values lower than 0.9 are not shown. Newly obtained sequences are underlined.

Table 1. Comparative characterisation of different isolates of *Apopharynx bolodes* based on some metric traits (in μm)

Characteristic	Braun (1902)	Odening (1962)	Our data
Locality	Kaliningrad Region, Russia	Berlin, Germany	Minsk Region, Belarus
Body size	2170 × 1000	3000 × 1260	1742–2309 × –
Oral sucker size	290 × 360	403 × 418	– × 282–324
Ventral sucker size	312 × 312	403 ^a	272–307 × 269–310
Anterior testis size	–	271 × 301	277–404 × 278–439
Posterior testis size	–	352 × 403	295–367 × 241–280
Ovary size	–	88 × 161	148–218 × 147–239
Eggs size	93 × 60–70	86–103 × 69–73	95 × –

^aDiameter.

(2022). However, the support for the second and the third clades in our tree was much lower than in the tree of Kalinina *et al.* (2022). The first of these main clades contains species of the Psilostominae Looss, 1900 (at least *P. limosum*), the second contains species of the Psilostominae and the Psilostomidae *incertae sedis* by Tkach *et al.* (2016), and the third contains species of the Psilostominae, the Apopharynginae, and the Sphaeridiotrematinae. Overall, our data, similarly to those of Kalinina *et al.* (2022), support the conclusion of

Kudlai *et al.* (2017) that the current subdivision of the Psilostomidae into subfamilies probably does not reflect true phylogenetic relationships of the psilostomid genera. The observed distribution of diagnostic characters of the Psilostominae Looss, 1900 between three major clades (i–iii) (see Kudlai *et al.* 2017; Kalinina *et al.* 2022) seems to indicate that the subdivision of the Psilostomidae into subfamilies should be completely abandoned. However, a final decision on this issue should be postponed until the accumulation of more molecular data on psilostomids.

Supplementary material. The supplementary material for this article can be found at <http://doi.org/10.1017/S0022149X24000543>.

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Competing interest. The authors declare that they have no competing interest.

Ethical standard. Not applicable. The host bird is a quarry species in Belarus, therefore ethical approval under the law of that country was not required.

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